INTERACTIONS BETWEEN THE BLACK REDSTART (*PHOENICURUS OCHRUROS*) AND ST. LUCIE CHERRY (*PRUNUS MAHALEB*) IN ROCKY HABITATS

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RÉSUMÉ

Nous avons étudié les interactions entre le Rougequeue noir (*Phoenicurus ochruros*) et le Bois de Sainte Lucie (*Prunus mahaleb*) dans deux zones rocheuses du nord-ouest de l'Espagne. Les Rougequeues noirs sont responsables d'à peu près 30 % de la consommation des fruits de *Prunus mahaleb* dans ces zones (604 observations sur un total de 1 854 données d'oiseaux s'alimentant sur 56 arbres, en 4 ans). En moyenne, 14 % des apports de nourriture aux poussins comportaient des fruits de *Prunus mahaleb* (7 à 28 % pour 8 nids en 3 ans). La proportion des becquées incluant des fruits était plus élevée durant la seconde moitié de la période de nourrissage des poussins que durant la première. En général, les oiseaux se posaient dans les rochers après avoir quitté les pieds-porteurs de *Prunus mahaleb* (74 % des cas). Des expériences de neuf mois sur la survie des graines effectuées dans la zone d'étude ont montré des différences significatives entre les trois types de substrat considérés (herbes, rochers et rochers sous le nid).

SUMMARY

We investigated interactions between the Black Redstart (*Phoenicurus ochruros*) and the St. Lucie cherry (*Prunus mahaleb*) in two rocky areas in northwest Spain. Black Redstarts are responsible for about 30 % of *P. mahaleb* fruit consumption in these areas (604 of a total of 1 854 observations of birds feeding; 56 trees, 4 years). On average 14 % of food deliveries to nestlings comprised *P. mahaleb* fruits (total 8 nests, 3 years; range for individual nests 7-28 %). The proportion of deliveries comprising fruits was higher during the second half of the nestling period than during the first half. Birds generally alighted on rock after leaving *P. mahaleb* plants (74 % of cases). Nine-month seed-survival experiments performed in the study area indicate significant variation among the three substrate types considered (grass, rock, rock-under-nest).

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INTRODUCTION

The assemblage of seed-dispersal frugivorous birds that feed on the fruits of a given species may show spatial variation at several scales: among populations within a region, among habitat patches within a population, and among individuals (Bronstein & Hoffmann, 1987; Guitian *et al.*, 1992; Jordano, 1993, 1994; Keeler-Wolf, 1988; Traveset, 1994). This variability is one of the most important factors for evaluating the final demographic consequences of the interaction between plants and frugivores at a local scale, and for understanding the evolutionary significance of mutualisms of this type, which are dependent on the constancy of the interaction (Jordano, 1994 and references therein).

What happens when the plant lives in an extreme environment? The typically low species richness of such environments should mean that few potential seed-dispersers are available and, consequently, that plants and seed dispersers may maintain particularly strong interactions.

In the present study, we describe an unusual interaction between a species of plant and a species of bird, both of which show a preference for rocky habitats.

Prunus mahaleb is a shrub which in Spain is largely restricted to regions of Mediterranean climate (Ceballos & Ruiz de la Torre, 1979). The study area is at the far northwestern limit of its range, where it occurs mainly on sunny, well-drained, stony sites. It frequently occurs on the rock-beds that accumulate at the base of steep-walled rocky gullies. The Black Redstart (*Phoenicurus ochruros*) is typically the commonest bird species in rocky habitats, throughout its area of distribution in northwest Spain. The plant bears mature fruits during June and July, coinciding with the period during which Black Redstarts are feeding their young both in the nest and as fledglings.

Given that *P. mahaleb* and the Black Redstart both occur in rocky habitats, the present study attemps to answer the following questions: 1) What role does the Black Redstart play in the dispersion of *P. mahaleb* seeds? 2) How important are *P. mahaleb* fruits in the diet of Black Redstart nestlings and fledglings? 3) Where do Black Redstarts transport *P. mahaleb* seeds? and 4) Do seedling survival rates differ depending on the substrate on which the seed is deposited? These questions were investigated basically by observational methods, though seedling survival rates on different substrates were investigated experimentally.

STUDY AREA

The study was carried out in two locations in northwest Spain, Portela and El Estrecho (Covas, Ourense Province), situated between 400 and 500 m a.s.l. in two valleys forming part of the River Sil watershed. Both are narrow gullies with limestone walls, cut into a flat meseta covered by holm oak (*Quercus rotundifolia*) scrub.

The Estrecho population of *P. mahaleb* is located along one side of the gully, and comprises about 150 individuals. The Portela population comprises about 50 individuals.

Black Redstarts breed at both sites (8 - 10 nests in Estrecho, 4 - 6 in Portela), generally in crevices and under overhangs in the rock walls of the gullies. In 1992, we measured the distance from each nest to each of the 20 nearest individuals of *P. mahaleb.*

MATERIALS AND METHODS

MONITORING FRUGIVORE VISITS AND FEEDING OF NESTLINGS

In June and July of 1990, 1992, 1993 and 1995, we monitored frugivore visits to trees in the study populations, recording all visiting bird species observed. In Portela, we monitored 8 trees in 1990 and 16 trees in 1992. In Estrecho, we monitored a total of 37 trees in 1992, 1993 and 1995. Each tree was observed for at least 4 hours.

During June and July of 1991, 1992 and 1993, we monitored feeding of Black Redstart nestlings in a total of 8 nests in the two sites, noting whether the food brought to the nest at each adult visit (henceforth referred to as a "food delivery") consisted of *P. mahaleb* fruits or other food items (basically insects and insect larvae). Identification of food items was generally straightforward, since birds typically use a routine series of perches before entering the nest. Sometimes, however, the bird entered the nest directly or perched only very briefly, so that it was not possible to identify the food item. Our estimates of the proportions of fruits in the diet are based on those cases in which it was possible to identify the food item. Nests were monitored for 4 - 30 hours each year, in each year over a 3- to 12-day period.

FEEDING OF FLEDGLINGS

In 1991,1992 and 1993 we monitored food deliveries to the fledglings of seven broods, close to the nest, noting whether the food brought consisted of fruits or other food items.

USE OF SUBSTRATES

While monitoring bird visits to trees, we also recorded the substrate subsequently used by Black Redstarts. Specifically, we recorded the first substrate alighted upon after leaving the tree, considering four categories: a) rock, including large boulders; b) stone-beds; c) trees or scrub, or tree- or scrub- bearing soil; d) grass.

SEED SURVIVAL

Starting 12 July 1991 we investigated seed survival using 12 batches of 30 *P. mahaleb* seeds. The seeds of each batch were placed on the ground in a 5×6 grid pattern (though see below), each seed being 1 m from its nearest neighbours; each batch was at least 40 m from the nearest other batch. Four batches (120 seeds) were placed on rock or stones. Another four batches were likewise placed on rock or stones, but close to Black Redstart nests that had been occupied that year (1 - 10 m from the nest). The last four batches were situated on soil without trees or shrubs and with scant herbaceous cover. The shape of the terrain beneath two of the nests made it impossible to lay the seeds out in a 5×6 pattern, so in these cases 15×2 patterns were used (again with 1 m between seeds). In all cases each seed

was fixed in position by gluing with a strong adhesive ("Superglue") to a 10-cm length of string, which was either glued directly to the substrate (in the case of rock or stones) or tied to a 10-cm length of thick wire that was driven into the ground. At the end of the experiment, none of the strings or wires had been detached from the substrate. Between 12 July 1991 and 29 December 1991, we visited the sites seven times (every 10 - 30 days), with a final visit on 10 March 1992, at each visit recording the number of seeds remaining in each batch. In almost all cases in which the seed was missing, part of the testa remained glued to the string, strongly suggesting predation.

RESULTS

About a third of *P. mahaleb* fruits consumed were consumed by Black Redstarts. This proportion remained roughly constant over the years of study, and differed little between the two sites (Tab. I). There was no significant variation among years in either of the populations (Portela: $\chi^2 = 3.41$, $p > 0.05$; Estrecho: $\chi^2 = 2.83$, $p > 0.05$).

Judging from the high proportion of food deliveries that contained *P. mahaleb* fruits (mean 13.9 %, sd = 4.78 %, data for 8 nests over 3 years), these formed a major component of the diet of chicks, though note that the range was wide (7.5 - 22.7 %, Tab. II). Considering the data for 1992 and 1993, during which several nests were monitored, the proportion of food deliveries comprising *P. mahaleb* fruits did not vary significantly among nests (1992: $\chi^2 = 4.49$, $p > 0.05$; 1993: $\chi^2 = 2.19$, $p > 0.05$). However, the proportion varied significantly among years ($\chi^2 = 11.2$, $p < 0.01$; 1991, 1992 and 1993, all nests).

TABLE I

Importance of the Black Redstart as a consumer of P. mahaleb *fruits in the study area, showing the total numbers of observations of fruit consumption (i.e. consumption of a single fruit) and the numbers due to Black Redstarts. Estimates of fruit abundance in each year and in each area are shown to the right.*

	Year	No. of trees	No. of observations (all birds)	No. observations (*Phoenicurus ochruros*)	%	Crop
Portela	1990	8	261	83	31.8	Abundant
	1992	16	544	211	42.2	Very abundant
Estrecho	1992	11	380	102	26.8	Very abundant
	1993	11	386	125	32.4	Abundant
	1995	15	283	83	29.5	Scant
Total		53	1 854	604	32.5	

Considering the four nests for which the total number of food deliveries identified was more than 100 (Tab. II), the proportion of deliveries comprising *P. mahaleb* fruits was higher in all nests during the second half of the nestling period than during the first half. Nevertheless, the difference was not statistically significant for any of the nests. There was no evidence of association between mean distance to the 20 nearest fruit-bearing trees and percentage of food deliveries comprising *P. mahaleb* fruits (Tab. II).

TABLE II

Summarized data on feeding of Black Redstart nestlings. The total number of hours of monitoring of each nest in each year, and the number of days over which these hours were distributed, is shown in the leftmost columns. The next three columns show the number of food deliveries comprising P. mahaleb *fruits, the number comprising insects, and the number whose content was not determined (nd). Also shown is the mean distance (sd) from the nest to the 20 nearest individuals of* P. mahaleb *(MD20NN).*

	Days	Hours	nd	Insects	Fruits (%)	MD20NN
1991						
Nest 1	8	24	97	163	48 (22.7)	
1992						
Nest 1	12	28	154	208	24 (10.3)	22.3 (7.5)
Nest 2	5	19	41	181	34 (15.8)	15.6 (3.6)
Nest 3	4	6	17	37	3 (7.5)	11.2 (3.1)
Nest 4	6	9	71	65	12 (15.5)	26.2 (8.6)
1993						
Nest 1	4	13	38	116	24 (17.1)	
Nest 2	3	6	14	30	4 (11.7)	
Nest 3	3	4	5	8	1 (11.1)	
Totals	45	149	437	808	150	

Chicks continued to be fed with *P. mahaleb* fruits after they had left the nest. Once they had left the immediate area of the nest, however, it was often not possible to determine which nest they had come from. As a result, all chicks were considered together during this period (1991, 1992 and 1993). Of the total of 109 deliveries observed to fledglings of a total of seven broods, 30 (27 %) comprised *P. mahaleb* fruits.

The Black Redstarts typically alighted on rock after leaving *P. mahaleb* plants (74 % of cases; Fig. 1). It is thus to be expected that a large proportion of the seeds consumed by adult birds will be regurgitated or defecated onto rock.

The area immediately surrounding the nest can likewise be expected to show a high density of *P. mahaleb* seeds, in view of the activity of adults and fledglings. The survival curves (Fig. 2) varied significantly among the three substrates (on rock under nests, on rock distant from the nests and on grassy sites, Gehan-

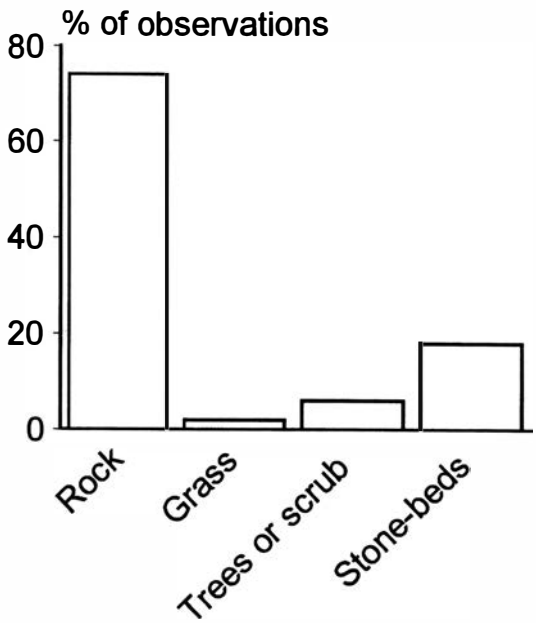

Figure 1. — Substrate use by Black Redstart: substrate alighted on after leaving *P. mahaleb* trees (529 observations).

Wilcoxon test, Tab. III), as did the proportion of seeds surviving 9 months after the start of the experiment ($\chi^2 = 11.2$, $p < 0.001$). This significant variation is largely attributable to the difference between "rock-under-nests" and the other two substrate types (Tab. III).

TABLE III

Results of application of the Gehan-Wilcoxon test (Pyke & Thompson, 1986) to test for the significance of differences between the seed survival curves shown in figure 2.

Sites types compared	Z	df	Significance level
Grass, rock, rock-under-nest	19.26	2	$p < 0.001$
Grass, rock	2.46	1	$p > 0.05$
Rock, rock-under-nest	10.96	1	$p < 0.001$
Grass, rocker-under-nest	15.7	1	$p < 0.001$

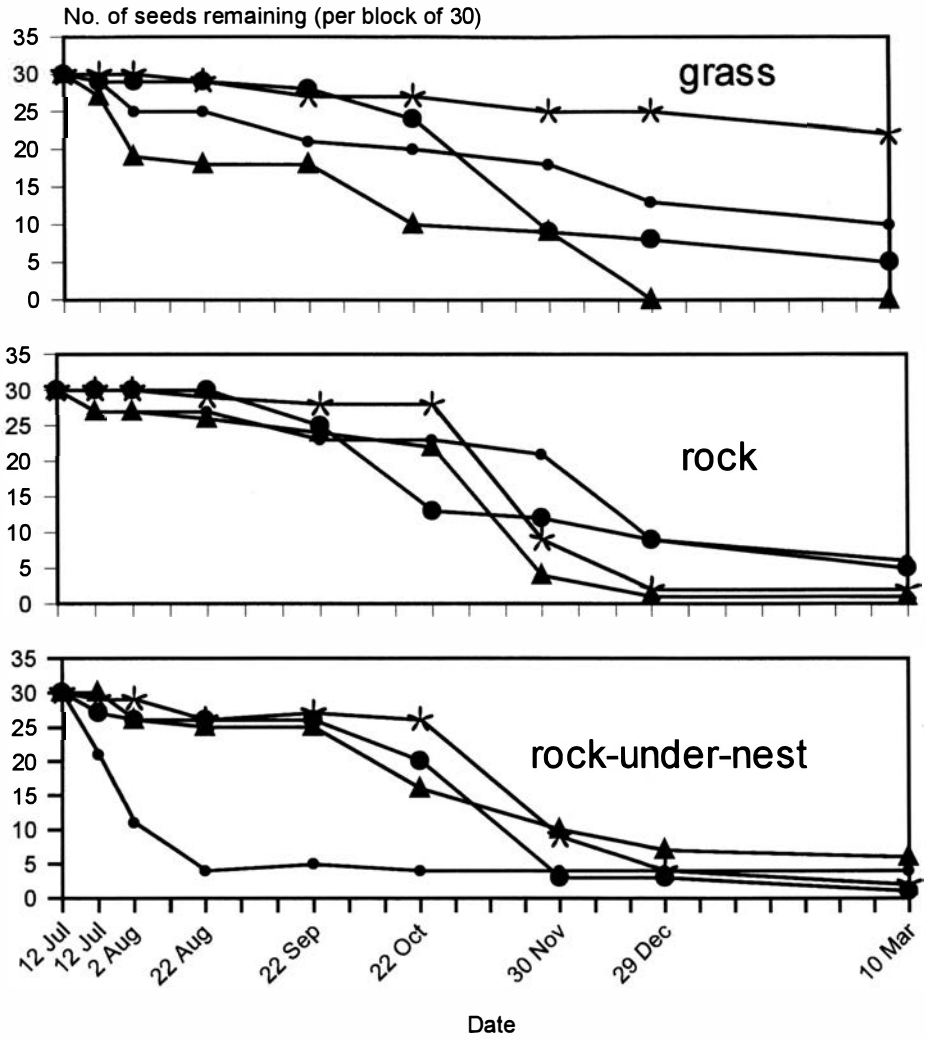

Figure 2. — Predation of *P. mahaleb* seeds on bare soil, rock and rock-under-nests between 12 July 1991 and 10 March 1992. A total of 120 seeds (4 blocks of 30) was laid out on each substrate. The vertical axis shows the number of seeds remaining on each day of monitoring.

DISCUSSION

The Black Redstart is one of the most important consumers of *Prunus mahaleb* at both sites studied, accounting for about 30 % of total consumption. This was true both in years of good fruit crop (e.g. 1992: 27 % of consumption in Estrecho, 42 % in Portela) and in years of poor fruit crop (e.g. 1995: 30 % in Estrecho).

The Black Redstart is at most a very occasional member of the bird assemblages visiting other fleshy-fruit-producing species in Western Europe (see for example Debussche & Isenmann, 1992; Fuentes, 1994; Guitian, 1984; Hernandez, 1993; Herrera, 1984; Jordano, 1984; Snow & Snow, 1988; Sorensen, 1981; Traveset, 1994). Indeed, this species only forms part of assemblages when the study area contains rocky habitats, as has been demonstrated previously by us (Guitian *et al.*, 1992) and by Jordano (1994).

In the present study, the Black Redstart was a more important consumer of *P. mahaleb* fruits (~ 30 %) than in Jordano's (1994) 8-year study in Cazorla (southeast Spain) (21 %) and Herrera & Jordano's (1981) study in another area of Cazorla (13 %). Our results, for two study sites which are effectively rock-walled gullies, clearly reflect an extreme case of an interaction which occurs basically because the habitats of the two species concerned coincide.

There is little published information about the feeding of fruits to the chicks of European passerines (though see Snow & Snow, 1988), and most of our current knowledge in this regard is based on studies in other regions (Beitwisch *et al.*, 1984; Skutch, 1976; Wheelwright, 1983, and references therein). Fruits are hardly ever the principal component of the diet, since their protein content is very low, whether in absolute terms (Morton, 1973; Snow, 1962; Snow, 1970) or with respect to caloric content (Ricklefs, 1976; Foster, 1978). The very few species of bird that are known to feed their young only with fruits, such as *Steatornis caripensis* and *Procnias averano*, have nestling periods that are much longer than in other species of similar size and characteristics (Snow, 1962; Snow, 1970).

Snow & Snow (1988) cite 14 species of wild and cultivated fruits in the diet of *Turdus merula* chicks in southern England, fruits of *Hedera helix* and *Prunus avium* being the most important. Within-season variation in the fruit species consumed reflected the availability of ripe fruits over the period April - August. In our study area, the only fruits ripe in June and early July, apart from those of *P. mahaleb*, are cherries (*Prunus avium sensu lato*) and a few *Rhamnus alaterna* fruits (most of which ripen in August). Despite the abundance of cherries, however, we have never seen Black Redstarts feeding chicks with these fruits, perhaps because they are too large for the Black Redstart's beak. We have seen Black Redstart chicks being fed with *Rhamnus alaterna* fruits on only two occasions.

In our study areas, there does not appear to have been a direct relationship between fruit availability in the immediate vicinity of a nest and the amount of fruits brought to that nest. The observed among-nest variation in the percentage of food deliveries comprising *P. mahaleb* fruits may in fact be attributable to differences in the behaviour of the individual adults concerned.

In general, our results are similar to those of Beitwisch *et al.* (1984), who investigated the diet of *Mimus polyglottos* chicks. The proportion of food deliveries consisting of fruits (largely of *Ficus* spp.) was similar to that observed in the present study. In addition, the proportion of deliveries comprising fruits increased over the nestling period, again as in the present study. An increase over the nestling period in the proportion of deliveries comprising fruits has likewise been reported in studies of *Pharomachrus mocinno* (Wheelwright, 1983; Avila & Velarde, 1996) and *Columba leucocephala* (Bancroft & Bowman, 1994), though no such tendency was detected in a study of *Euphonia hirundinacea* (Sargent, 1993).

Within our study area, Black Redstarts acted as genuine seed-dispersers. Of the fruits manipulated, only about 4 % are dropped, while 7 % are transported and the rest swallowed while at the tree (Rodriguez & Bermejo, 1995). These findings, together with the results of the present study (which suggest that about a third of *P. mahaleb* fruits consumed in the study area are consumed by Black Redstarts, and that the seeds of most of these fruits end up on rock) suggest that about a third of the *P. mahaleb* seeds will end up on rock, following passage through the digestive tract of an adult or chick. In the first case, a significant proportion of seeds end up in cracks in the rock. The fate of seeds of fruits transported to the nest is rather more complicated. We have inspected a total of 42 Black Redstart nests (both recently abandoned and from previous years, in the study area and nearby areas), and have never found any *P. mahaleb* seed either in the nest itself or in the crevice which houses it. This suggests that seeds defecated by nestlings are either eaten by seed predators (this seems unlikely, since no seed remains were found in our nest inspections) or removed from the nest in faecal sacs by the adults (see Simons & Simons, 1993). We have some observational data in this regard: of a total of 53 faecal sacs that clearly contained fruits (in view of their purplish colour), 42 (79 %) were deposited 10 to 40 m from the nests (mean 31.3 m; standard deviation 15.9 m).

The use of rocky substrates by the Black Redstart in areas where it feeds on *P. mahaleb* fruits is habitual, and the possible implications of this behaviour for seed dispersal have been commented on previously (Herrera & Jordano, 1981; Schupp, 1992). In the present study, Black Redstarts perched on rock more frequently (about 70 % of observations) than in both these previous studies; this is not only because rock is the principal substrate in our study area, but also because rock is the Black Redstart's preferred substrate. *Turdus merula*, for example, another important disperser of *P. mahaleb* seeds in our study area (Guitian *et al.*, 1992), perched on rock much less frequently (about 40 % of 383 observations; unpublished observations).

The observed between-substrate differences in our seed survival experiments provide evidence of spatial variation in post-dispersal predation, as reported in a number of previous studies (for example Schupp, 1988a, 1988b, 1990; Whelan *et al.*, 1991). Mean overall seed predation rates 9 months after the start of the experiment (82 %, sd = 20 %) are similar to those obtained by Whelan *et al.* (1991) in Illinois (USA), in experiments in which seeds of *Cornus drummondi* and *Prunus serotina* were exposed to predation for 60 days.

In the present case, our results suggest that one of the chief sources of variability may be increased predation under nests, either because small rodents tend to be more abundant in these areas, or because they typically forage for seeds in these areas.

In conclusion, our results indicate that the Black Redstart is one of the principal dispersers of seeds of *P. mahaleb* in the study area. A large proportion of the seeds deposited on rock suffer predation, but many of those that survive and germinate are probably in a favourable location, since the rocky sites are often sunny and well-drained, and with little competition from other trees (note that *P. mahaleb* is here at the northern limit of its range). Our results also indicate that the fruits of *P. mahaleb* are important in the diet of adults, nestlings and fledglings of Black Redstart. Nevertheless, we are unaware of such close relationships between *P. mahaleb* and Black Redstart in other areas of their ranges, and the

existence of a relationship in the study area is probably best viewed as an incidental result of the habitat overlap of these two species in our region.

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